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Model-Aided Understanding of Harmful Algal Blooms

(有害藻類開花のモデル支援解析）

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Abstract

１．Background, problem statement and objective

The term harmful algal bloom (in short, HAB) indicates an algal bloom that has negative impacts on other organisms via the production of toxins, mechanical damage, or by other means. HAB include different types of taxa such as dinoflagellates, diatoms, and cyanobacteria (blue-green algae). The latter are of special importance because of their potential impact on drinking or recreational waters. In fact, they can produce a variety of potent toxins called *cyanotoxins*. These compounds have been found to be hepatotoxic or neurotoxic for a wide range of organisms, including humans. Therefore, in the recent years, the formation of toxic blooms of cyanobacteria in lakes and rivers has been causing more and more concern. Ecological evidence suggest that toxic and nontoxic species of freshwater phytoplankton hardly coexist in absence of other species. In particular, competition experiments have shown that the toxic strain of *Microcystis* is a very poor competitor for light. Although the mentioned experiment dealt with one particular genus, toxin-producing planktonic species are expected to be poor competitor for resources in general. However, experimental results suggest that increments in temperature and changes in the ratios of nutrients might reverse the situation. These evidence suggest that toxic and nontoxic species of freshwater phytoplankton hardly coexist in absence of other species. Then how can these species survive and actually bloom? Toxin-producing *Microcystis* has overall an inhibitory effect on the growth of most herbivore taxa. Nevertheless, zooplankton usually grazes on both toxic and nontoxic species. In particular, while a few species like the rotifer *Brachionus calyciflorus* and the cladoceran *Bosmina longirostris* apparently make no great distinction between toxic and non toxic prey, the feeding rates of other small-bodied cladocerans, rotifers, and copepods seem to be strongly related to the toxicity of *Microcystis*. In view of these observations, we consider predator and toxic prey to have an inhibitory effect on each other. It is suggested in the literature that toxicity to planktonic grazers has a very protective value: it reduces the grazing pressure directly (a fast mechanism), and it lowers the population density of predators (a long lasting effect). Some authors propose that the formation of surface blooms of *Microcystis* is strongly connected to the presence or absence of zooplankton, and to its selective predatory activity. In fact, these authors observed that if the zooplankton was removed from the water at the start of the experiment, no surface bloom of *Microcystis* appeared regardless of the addition of nutrients. The naive question is: can the existence of such interaction promote the spatial pattern formation and local algal blooms? This ecological question motivates us to theoretically understand the mechanism behind the formation of spatial blooms of toxic plankton. To this end, in this thesis we propose a two-prey (toxic and nontoxic phytoplankton)-one-predator (zooplankton) Lotka-Volterra system with diffusion, for which it is assumed that the toxic prey is a weaker competitor than the non-toxic one for common resources in absence of the predator. Further, it is assumed that, depending on the toxicity and another parameter, the predator is more or less inclined to avoid the toxic prey. Previous studies have shown that the classical one-prey and one-predator Lotka-Volterra system never exhibits spatial pattern formation, while higher nonlinearities such as Allee effect can induce such a phenomenon. Thus, a complicated functional response is a candidate for the mechanism of spatial blooms. Biologically, other

factors such as the spatial variation in light, nutrients and water temperature might also play an important role. Here we study another possibility. Can spatially local blooms be explained only by the presence of toxin producing species that have a negative effect on the growth of zooplankton? To answer this question, we will study analytically and numerically the reaction-diffuion system.

2. Summary of the chapters and conclusion

After a preliminary analysis of the ordinary differential equations, carried out in the first chapter, we will focus on the reaction-diffusion system in order to study its spatiotemporal dynamics. Our goal is to show the effect of the existence of toxin-producing phytoplankton species on the spatial pattern formation and to investigate how the formation of toxic blooms is related to the selective predatory activity of zooplankton. Toward this goal, in the second chapter we will perform the bifurcation analysis and numerical calculations of the reaction-diffusion system showing the emergence of spatially local blooms of toxin-producing phytoplankton in dimensions one and two, due to diffusion-driven instability.

From the third chapter, we will restrict ourselves to the 1-dimensional problem and investigate the global bifurcation structure of the equilibrium points. We will show that interesting phenomena such as the occurrence of hysteresis loops and the coexistence of multiple stable non-constant stationary solutions occur. In particular, these findings will shed light on the insufficiency of the linear stability analysis that was performed in the previous chapters and hence improve the results till there presented. The final chapters of this work will be dedicated to the derivation and the analysis of the shadow system associated to the reaction-diffusion system, that is, we will consider our original problem in the limit where the diffusion of the predator goes to infinity under the assumption of boundedness of the solutions. In chapter 4 we will show the existence of the solutions of such limiting system by employing analytical and semi-analytical methods. Moreover, theorems regarding the existence and stability of the solutions will be given. In the final chapter will discuss the applicability of the shadow system as an approximation of the original problem with respect to the size of the domain.

Conclusion

The aim of this thesis was to study freshwater harmful algal blooms through a mathematical modeling approach. In order to have a better understanding of how and why such blooms occur, we have proposed a model of reaction-diffusion equations in which one prey has a toxic effect on the predator that inhibits its growth.

In the first two chapters we have performed linear stability analysis of the ode and the pde, and shown that blooms of cyanobacteria may be triggered by diffusion-driven instability. We have also discussed a function that describes the avoidance behavior of the predator and connected such behavior to the formation of blooms. The global bifurcation analysis performed in chapter 3 revealed the insufficiency of the analysis of the first two chapters. In fact, we found out that blooming may occur even when the 3-species coexistence equilibrium is stable in the reaction-diffusion system. Moreover, interesting facts such as the coexistence of multiple stable non-constant stationary solutions and the occurrence of hysteresis loops were revealed.

In chapter 4 we formally derived the shadow system, proved the existence and stability of the solutions, and shown its applicability as an approximation of the original problem (in a smaller domain size with respect to the one originally considered). Finally, we have investigated the applicability of this limiting system and discussed when it gives a good approximation of the original problem depending on the domain size. We have found out that larger domain sizes imply a worse approximation (unless extremely large diffusion coefficients are considered). Under a biological perspective this means that the shadow system might offer a good approximation tools for small lakes, rather than for larger systems. In general, the results of this thesis, are consistent with several experimental results regarding for example the avoidance behavior of zooplankton and the formation of blooms. We suggest that the ability of zooplankton to move faster and to direct its grazing effort mainly on the nontoxic prey might be one of the mechanisms underlying the spatial formation of these toxic blooms.